# Revised Nomenclature and a New North American Record for the Villose Cliff Brake (*Pellaea*, Pteridophyta)

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ABSTRACT. Originally described by Fée in 1857, the villose cliff brake was not validly published for another 136 years. In 1993, this member of the Pteridaceae (*sensu* Tryon & Tryon) was named *Pellaea ternifolia* subsp. *villosa* Windham, acknowledging its overall similarity to the ternate cliff brake. Although formally including it within *P. ternifolia* (Cavanilles) Link, Windham suggested that the villose cliff brake was a probable allotetraploid produced by hybridization between typical *P. ternifolia* and some other (then unidentified) taxon. Recent work by Mendoza et al. has identified a new species, *P. ribae* Mendoza & Windham, that appears to be the "missing parent." Considering the evidence that the villose cliff brake is a reproductively competent taxon that originated as a hybrid between *P. ternifolia* subsp. *ternifolia* and *P. ribae*, we now feel that it should be recognized as a distinct species. Herein, we propose a new combination, *Pellaea villosa* (Windham) Windham & Yatskievych, for the villose cliff brake. We also report a northern range extension to Arizona, the second record for the area covered by the *Flora of North America*.

*Key words:* Arizona, North America, *Pellaea*, Pteridaceae.

While preparing a taxonomic treatment of *Pellaea* for Volume 2 of the Flora of North America Project (Windham, 1993b), the senior author determined that U.S. populations assigned to *Pellaea ternifolia* (Cavanilles) Link (Pteridaceae: subfam. Cheilanthoideae, *sensu* Tryon & Tryon, 1982) represent "three genetically distinct taxa characterized by differences in leaf morphology and chromosome number" (Windham, 1993a: 42). The most distinctive element, a tetraploid with sparsely villous fronds, was segregated as *P. ternifolia* (Cavanilles) Link subsp. *villosa* Windham, the villose cliff brake. Reported from a single locality within the boundaries of the *Flora* (Windham, 1993b), this taxon is relatively widespread in Mexico and probably originated there (Windham, 1993a). Considering this distribution, it is not surprising that subsequent work on the pellaeas of Mexico (Mendoza et al., 2001; Mickel, in press) has substantially improved our understanding of *P. ternifolia* subsp. *villosa*. These new data require a reconsideration of both the taxonomy and the known distribution of this taxon.

*Pellaea ternifolia* was first described (as *Pteris ternifolia* Cavanilles) in 1802. It has the most extensive distribution of any species in the genus, ranging from the southwestern United States to southern Chile, with disjunct populations in Hawaii and Hispaniola (Tryon, 1957). Within this vast range, there is considerable habitat diversity and ample opportunity for geographic isolation. These factors have combined to produce a puzzling array of morphotypes and an equally complex synonymy (Tryon, 1957: 150). Nearly all of the synonyms and proposed segregates have essentially glabrous leaves like the type material of *P. ternifolia* from Peru (*Née s.n.*; lectotype [designated by Christensen, 1937]: MA not seen; isolectotype: F). The first author to discuss the villose cliff brake *per se* was Fée (1857), who provided an accurate description and the provisional name "P. lanuginosa." Although impressed by the apparent distinctness of this taxon, Fée merely discussed it under *P. ternifolia* and stated that he wanted to see more material before recognizing it formally. Thus, the name "P. lanuginosa" Fée was considered a *nomen provisorium* by Tryon (1957), and has never been validated.

Since Fée's initial recognition of the villose cliff brake, its distinctive nature has become more evident. Alice Tryon noted a correlation between chromosome number and leaf morphology in *Pellaea ternifolia*, stating that "the tetraploid plants gen-

Table 1. Comparison of selected taxa belonging to the *Pellaea ternifolia* complex demonstrating the intermediacy of *P. villosa*. The characters listed for *P. ternifolia* apply only to the diploid cytotype of subspecies *ternifolia* (see text).

| Characters | *P. ternifolia* | *P. villosa* | *P. ribae* |
|---|---|---|---|
| Rhizome scale shape | Linear-subulate | Linear | Linear-filiform |
| Rhizome scale length | 5–7 mm | 6–12 mm | 8–15 mm |
| Rhizome scale coloration | Bicolored | Mostly bicolored | Concolored |
| Petioles and rachises | Glabrous or with a few scattered trichomes | ± Villous | Densely villous |
| Distal portion of petioles | Grooved or flattened adaxially | Rounded to slightly flattened adaxially | Rounded adaxially |
| Pinnae | Ternately divided except at leaf apex | Usually entire for distal ⅓–½ | Entire throughout |
| Abaxial pinna surfaces | Glabrous | Sparsely villous | Densely villous |
| Apical mucro on pinnae | Well-developed | Weakly developed | Absent |
| Largest ultimate segments | Usually <18 mm long | Usually >18 mm long | Usually <18 mm long |
| Mean spore size | 39–45 μm | 46–53 μm | 53–60 μm |
| Chromosome number | $n = 29$ (diploid) | $n = 58$ (tetraploid) | Unknown |

erally resemble the diploids, but the pinnae tend to be entire and the rachises more pubescent" (Tryon, 1972: 230). Based on isozyme profiles and additional chromosome studies, the senior author suggested that the "tetraploids are segmental allopolyploids produced by hybridization between typical *P. ternifolia* and other (as yet unidentified) diploid elements within the *P. ternifolia* complex" (Windham, 1993a: 42). With no specimens of the "missing parent" at hand, Windham (1993a, 1993b) took a conservative approach to the taxonomy of the group and recognized the villose cliff brake as a subspecies of *P. ternifolia*.

Subsequent work on the cliff brakes of Mexico (Mendoza et al., 2001; Mickel, in press) indicates that this classification needs revision. Central to our change in thinking is the discovery of *Pellaea ribae* Mendoza & Windham (Mendoza et al., 2001), the probable "missing parent" of the villose cliff brake. As shown in Figure 1 and Table 1, subspecies *villosa* is morphologically intermediate between diploid *P. ternifolia* subsp. *ternifolia* and *P. ribae* in nearly every character examined. From minute details of the rhizome scales to the more obvious features of frond dissection and pubescence, the villose cliff brake exhibits clear intermediacy. The only exception is in the length of the largest ultimate segments. These usually exceed 18 mm in subspecies *villosa* and are usually less than 18 mm in both diploid *P. ternifolia* subsp. *ternifolia* and *P. ribae* (Table 1). Such increases in frond segment size are common in hybrid ferns (e.g., Windham, 1988; Paler & Barrington, 1995) and may be attributable to heterosis (Grant, 1975).

Although morphological intermediacy is expected in taxa of hybrid origin, it rarely extends to mean spore size, as it does in the case of the villose cliff brake (Table 1). In general, allotetraploid ferns produce spores that are somewhat larger than either parent due to increased DNA content. The lack of a chromosome count for *Pellaea ribae* leaves open two possibilities. If spore sizes are strictly correlated with ploidy level in this group, then the materials of *P. ribae* currently at hand likely represent a polyploid derivative of the "missing parent" of subspecies *villosa*. Alternatively, *P. ribae* may exemplify a rare exception to the correlation between chromosome number and spore size. The species appears to be a strict gypsophile, and larger propagules might provide an adaptive advantage in such a harsh habitat. *Notholaena bryopoda* Maxon, another strict gypsophile that is known to be diploid, also has exceptionally large spores (Windham, unpublished). Plants of *P. ribae* derived from spores of the type collection currently are being grown at the Missouri Botanical Garden in hopes of testing these hypotheses.

Regardless of the actual chromosome number of *Pellaea ribae*, the data at hand indicate that the features distinguishing subspecies *villosa* from typical *P. ternifolia* derive from a genome shared with *P. ribae*. This genome is strikingly divergent from that of diploid *P. ternifolia*, confirming the suggestion (Windham, 1993a) that the villose cliff brake is an allotetraploid. Although subspecies *villosa* was formed originally by interspecific hybridization between *P. ternifolia* and *P. ribae*, we contend that it is a reproductively competent allopolyploid taxon

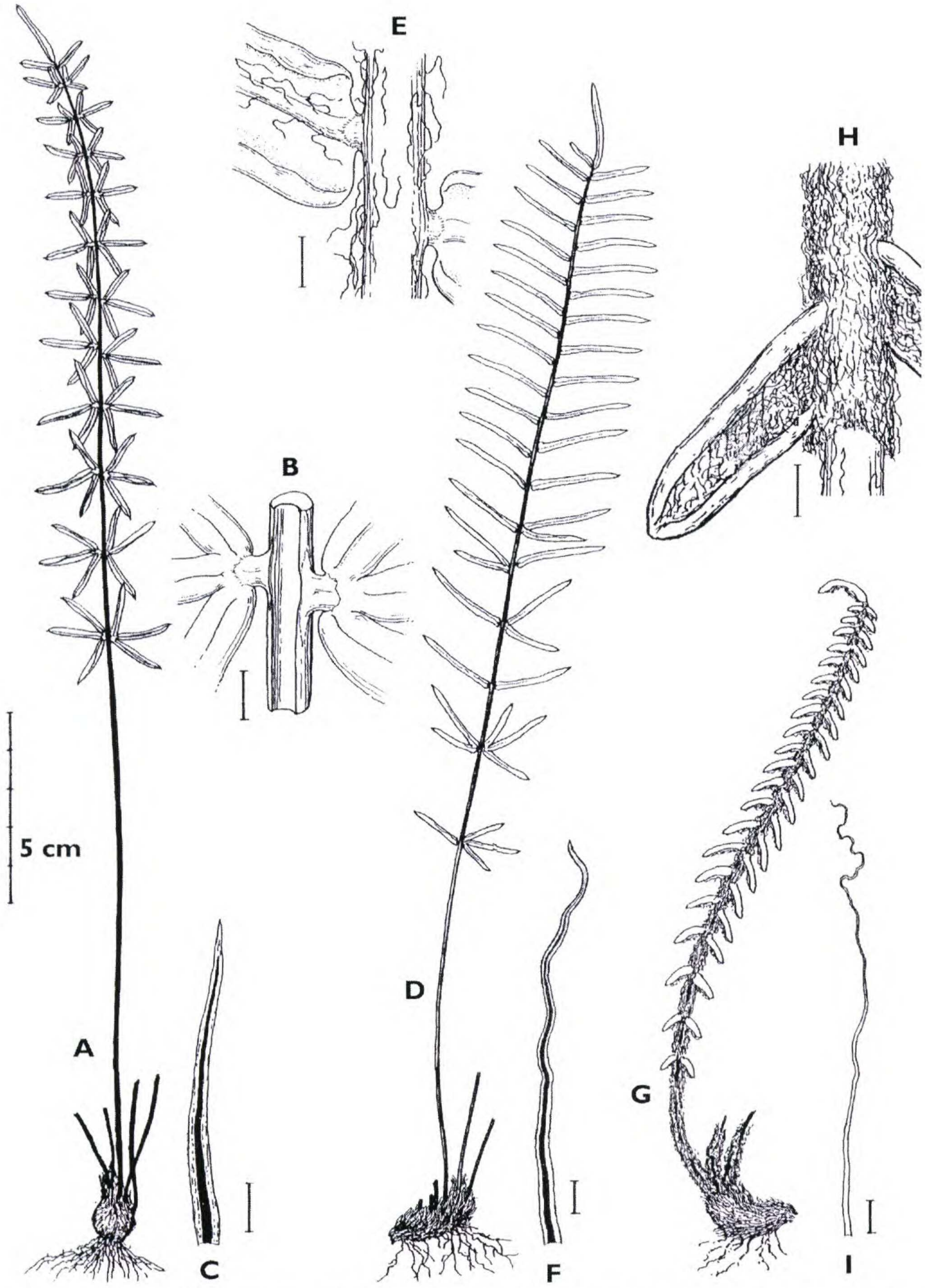


Figure 1. A–C. Diploid *P. ternifolia* (Cav.) Link subsp. *ternifolia* drawn from *Mickel 3849* (NY). —A. Leaf and rhizome. —B. Rachis and pinna attachment (adaxial surface). —C. Rhizome scale. D–F. *P. villosa* (Windham) Windham & Yatskievych drawn from *Rzedowski 22894* (NY). —D. Leaf and rhizome. —E. Rachis and pinna attachment (abaxial surface). —F. Rhizome scale. G–I. *P. ribae* Mendoza & Windham drawn from *Heil 5347* (BRY). —G. Leaf and rhizome. —H. Rachis and pinna attachment (abaxial surface). —I. Rhizome scale. Scale bar = 5 cm (A, D, G), 1 mm (B, C, E, F, H). Adapted from Mickel (in press).

that should be treated taxonomically as a separate species. It is amply distinct morphologically from both *P. ternifolia* and *P. ribae* (Table 1).

The appendix on nothotaxa in the *International Code of Botanical Nomenclature* (Greuter et al., 2000) states in Article H.5.1, "The appropriate rank of a nothotaxon is that of the postulated or known parent taxa." However, Article 5.2 states, "If the postulated or known parent taxa are of unequal rank, the appropriate rank of the nothotaxon is the lowest of these ranks." Given that we postulate that *P. villosa* arose following hybridization between a subspecies of *P. ternifolia* and the species *P. ribae*, these statements might be interpreted to require the continued recognition of *P. villosa* at the subspecific rather than specific level. We draw attention to problems of interpretation created by this section of the *Code*, especially as applied to fern nomenclature. The present practice among biosystematists, including most pteridologists, is to distinguish between primary hybrids and the reproductively competent taxa (sensu Wagner, 1954) that evolve from them following polyploidization. Such allopolyploids are reproductively isolated from either parent and function as full species; therefore we believe they should not be treated nomenclaturally as hybrids.

Although we considered validating Fée's *nomen provisorium* for this taxon, we have not seen the type (staff at P were unable to locate the specimen). Thus we are uncertain as to the precise application of the name. We therefore propose the following new combination based on the epithet applied by Windham (1993a):

**Pellaea villosa** (Windham) Windham & Yatskievych, comb. et stat. nov. Basionym: *Pellaea ternifolia* (Cavanilles) Link subsp. *villosa* Windham, Contr. Univ. Michigan Herb. 19: 43. 1993. TYPE: Mexico. Hidalgo: rocky hills, Lena Station, 8300 ft., 24 Aug. 1905, *C. G. Pringle 10025* (holotype, LL; isotypes, ARIZ, BRY, CAS, COLO, DAO, ENCB, F, GH, IND, KANU, LL, MSC, OKLA, SMU, TEX, UC, US, VT, WIS).

This species, occurring on various rocky substrates, is widespread in the Sierra Madre Occidental and Sierra Madre Oriental of northern and central Mexico. Mickel (in press) has identified specimens from the states of Chihuahua, Coahuila, Durango, Guanajuato, Hidalgo, México, Michoacán, Nuevo León, Puebla, San Luis Potosí, and Sonora. In the United States, the villose cliff brake has been reported from a single locality in the Davis Mountains of western Texas (Windham, 1993b). However, recent botanical surveys of the Madrean "sky islands" of southern Arizona have identified a second U.S. population:

U.S.A. **Arizona:** Cochise Co., Huachuca Mountains, Lone Mountain Watershed, Sycamore Canyon, above Mud Spring, 31°24′N 110°23½′W, elev. 5700 ft., E-facing slope just above arroyo bottom in pine-oak woods with *Juniperus deppeana, Quercus emoryi, Eragrostis, Muhlenbergia emersleyi, Cyperus, Bouteloua, Tradescantia, Ranunculus arizonicus, Ipomoea, Calliandra, Bommeria*, terrestrial; uncommon, 11 Aug. 1996, *M. Fishbein 2861, with K. Hooper & R. Coleman* (ARIZ).

This new population is situated approximately 300 km north to northwest of the closest known localities in the Sierra Madre Occidental and 600 km west-northwest of the only other U.S. collection site. It remains to be seen whether *Pellaea villosa* will be found in the mountains of southern New Mexico, which have fewer Madrean habitats. At the moment, it belongs to a group of species (including the ferns *Cheilanthes lendigera* (Cavanilles) Swartz, *Notholaena aschenborniana* Klotzsch, *N. neglecta* Maxon, and *P. ternifolia* (Cavanilles) Link subsp. *arizonica* Windham) that are known from Arizona and trans-Pecos Texas but not from intervening regions of New Mexico.

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